FOLIAGE AGE AS A FACTOR IN FOOD UTILIZATION BY THE WESTERN SPRUCE BUDWORM, *CHORISTONEURA OCCIDENTALIS*

Elizabeth A. Blake[1] and Michael R. Wagner[1]

ABSTRACT.—The influence of current year foliage age on food consumption and utilization by the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera:Tortricidae), was examined. Larvae were fed immature foliage of Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), Engelmann spruce (*Picea engelmannii*), and corkbark fir (*Abies lasiocarpa* var. *arizonica*) in June and August of 1981 and Douglas fir in June and July of 1982. All larvae feeding on early season (June) foliage reached maturity. Larvae feeding on middle (July) and late (August) season foliage died before reaching pupation. Relative growth rate and efficiency of conversion of ingested food decreased with foliage age in both the 1981 and 1982 experiments. Relative consumption rate increased with foliage age in the 1981 and decreased in the 1982 experiment.

The normal free-feeding period for western spruce budworm, *Choristoneura occidentalis* Freeman, larvae begins in early spring at host bud burst. The larvae feed primarily on immature host foliage, ingesting mature foliage only when the preferred diet is unavailable. Nutrient content and ease of ingestion and digestibility are often greater in immature foliage than in mature foliage (Heron 1964, Scriber and Slansky 1981). Host defenses such as lignins, silica, tannins, oils, waxes, and resins often increase with foliage age. Such changes in food quality may be responsible for the western spruce budworm's preference for early season foliage.

The purpose of this study was to determine the influence of the age of current year foliage on consumption and utilization by the western spruce budworm.

METHODS

Feeding experiments were conducted 13 June-4 July and 10 August-25 August in 1981 and again 16 June-10 July and 10 July-30 July in 1982. Larvae were collected from the field and reared individually in 150 × 25 mm petri dishes at 16L:8D and 24–26 C during the feeding experiments. Sixteen replicates were set up for each year and season. Host tree and larvae selection and calculation of nutritional indices followed Wagner and Blake (1983). Collection of larvae and foliage, preparation of foliage for feeding, and calculation of ingested foliage differed in 1981 and 1982.

To standardize the host phenological stage, early season feeding experiments were begun when the foliage was at the "brush" stage (bud cap gone, needles flaring but no shoot growth so needles appear to arise from one location) (Shepherd 1983). The middle season feeding experiment conducted in 1982 was begun after all the larvae used in the early season experiment had pupated. The 1981 late season feeding experiment was conducted in early August, after the natural insect population had ceased feeding in the field.

1981 Feeding Experiment

When *C. occidentalis* larvae were collected in the field, no attempt was made to segregate them based on the host foliage from which they were collected. Third instar larvae were selected for the first seasonal experiment using head capsule measurements (Bean and Batzer 1957, Wagg 1958). The remaining larvae were reared to pupation, mated, and allowed to oviposit. When the eggs hatched, the larvae were placed on artificial diet to feed. Those larvae that did not diapause were selected from the population and reared to the fourth instar on artificial diet. Larvae were moved to natural foliage 48 hours before the second seasonal experiment was begun. A minimum of 24 hours was necessary for successful acceptance and assimilation of a food

[1]Northern Arizona University, School of Forestry, Flagstaff, Arizona 86011.

source by the budworm larvae (Jacqueline Lee Robinson, personal communication).

Foliage was collected at random from the lower crown of Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, corkbark fir, *Abies lasiocarpa* var. *arizonica* (Merriam) Lemm., and Engelmann spruce, *Picea engelmannii* Parry ex. Engelm. trees located approximately 16 km north of Flagstaff, Arizona. Previous years' needles were clipped from the stem, and the twigs, with only current year foliage attached, were weighed.

The foliage twigs were replaced every 72 hours, and the twigs that had been fed upon were oven dried (60 C until no further weight loss occurred) and weighed. Foliage ingested was calculated on a dry weight basis as follows:

$$W_I = (W_F \cdot X)_B - DW_A$$

where:

W_I = dry weight of foliage ingested (mg)

W_F = fresh weight of the foliage twig before feeding (mg)

X = % dry weight of an aliquot foliage twig

DW_A = dry weight of the foliage twig after feeding (mg)

The aliquot twig used to calculate the initial dry weight of each feeding twig was selected for uniformity in size and phenological stage from the same host tree that provided the feeding twig.

Each replicate was terminated at pupation or when the larvae stopped feeding. Pupae and total feces for each replicate were oven dried and then weighed. Total foliage ingested was calculated and duration was noted for each replicate. Data were analyzed using a one-way analysis of variance (AOV) with alpha equal to 0.10.

1982 Feeding Experiment

Third instar larvae were collected from Douglas-fir trees in the Kaibab National Forest, North Kaibab Ranger District, Arizona. Larvae used for the early season experiment were allowed to feed on Douglas-fir foliage and advance to the fourth instar. Larvae used for the middle season feeding experiments were placed in cold storage at the time of collection to retard their development. These larvae were brought to room temperature five days before the experiment was to begin and allowed to advance to the fourth instar.

Foliage used for the 1982 feeding experiment was collected from a single medium vigor (Waring et al. 1980) Douglas-fir tree. Paired foliage samples, selected for uniformity in size and phenology, were collected from midcrown at the four cardinal directions. One twig was used to determine the average dry weight per needle; the other foliage twig was used to feed one budworm larva. The average weight per needle was later used to estimate the dry weight of the foliage consumed by the insect. Foliage was replaced every 72 hours to assure freshness and acceptability.

Each replicate was terminated at pupation or when feeding ceased. Total foliage ingested was calculated; pupae and feces were oven dried and then weighed. After calculating the nutritional indices, data were analyzed using a one-way AOV, with alpha equal to 0.10.

RESULTS AND DISCUSSION

Total foliage ingested was eliminated from the data analysis because the length of feeding time was highly variable between the feeding seasons. Nutritional indices for early, or normal, season feeding were calculated for larvae that had pupated. All the larvae feeding on middle (1982) and late (1981) season foliage died before reaching pupation. However, the nutritional indices were still calculated for larvae that fed for at least 10 days. The percent of larvae that survived until pupation was calculated for each experiment.

Results of the 1981 experiment using Douglas-fir foliage showed significant differences between early and late season foliage for all the nutritional indices calculated (Table 1). Budworms feeding on late season foliage appear to have increased their relative consumption rate (RCR) to compensate for a decrease in efficiency of conversion of ingested food to body weight (ECI). Despite this effort, *C. occidentalis* larvae were unable to maintain a relative growth rate (RGR) statistically equal to budworms feeding on early season foliage.

Larvae feeding on Engelmann spruce foliage followed the same pattern of food utilization as larvae feeding on Douglas-fir foliage

TABLE 1. Effect of Douglas-fir foliage age on food utilization by western spruce budworm (1981).

Season	Survival %	Food utilization indices: Relative consumption rate	Relative growth rate	ECI
Early (16,4)[b]	25	3.00 A[a]	0.09 A	5.08 A
Late (16,4)	0	9.28 B	0.01 B	0.16 B
F-Prob.		0.07	0.02	0.02

[a]One-way AOV, α = 0.10, values followed by different letters are significantly different.
[b]Numbers in parentheses are, respectively, initial number of larvae and number of larvae used to calculate nutritional indices.
ECI = Efficiency of ingested food to body weight.
Designations apply for three following tables.

TABLE 2. Effect of Engelmann spruce foliage age on food utilization by western spruce budworm (1981).

Season	Survival %	Food utilization indices: Relative consumption rate	Relative growth rate	ECI
Early (16,3)	19	1.33 A	0.15 A	11.65 A
Late (16,2)	0	4.19 B	−0.05 B	− 1.34 B
F-Prob.		0.01	0.01	0.01

TABLE 3. Effect of corkbark fir foliage age on food utilization by western spruce budworm (1981).

Season	Survival %	Food utilization indices: Relative consumption rate	Relative growth rate	ECI
Early (16,2)	13	2.67 A	0.13 A	4.78 A
Late (16,5)	0	4.70 A	0.06 A	3.24 A
F-Prob.		0.50	0.24	0.56

TABLE 4. Influence of Douglas-fir foliage age on food utilization by western spruce budworm larvae (1982).

Season	Survival %	Food utilization indices: Relative consumption rate	Relative growth rate	ECI
Early (16,6)	38	1.58 A	0.08 A	5.08 A
Middle (16,2)	0	1.05 B	−0.08 B	−8.02 B
F-Prob.		0.02	0.0002	0.0014

(Table 2). Although their average RCR increased significantly, the mean larval weight was significantly lower in the late season experiment when compared to the mean weight of larvae reared on early season foliage. In fact, the larvae that were fed late season foliage lost weight, probably as a result of a negative average ECI.

No significant differences were found between seasons for the three indices reported when *C. occidentalis* larvae were fed corkbark fir foliage (Table 3). However, the pattern of change in food utilization was similar to the results of the experiments using Douglas-fir and Engelmann spruce.

Significant differences were found in utilization between early and middle season feeding in 1982 (Table 4). RGR and ECI decreased significantly, which follows the pattern of the 1981 experiment. However, RCR also decreased significantly during the middle season feeding rather than increasing as predicted by Waldbauer (1968) and the 1981 feeding experiments. The larvae may have encountered chemical or physical feeding deterrents in the middle season foliage that resulted in low RCR. This result could also have been due to the period of cold storage used to slow larval development, which may have been retarded to the point where the larvae could not recover.

The statistical results of the foliage age experiments conducted in 1981 and 1982 can only be compared as to their relative patterns. Actual numbers should be disregarded due to the inconsistency in initial larval stage.

CONCLUSIONS

Host foliage phenology appears to greatly influence the food utilization and developmental success of *C. occidentalis*. Although no chemical tests were conducted on the foliage used for these experiments, the significant changes in RCR, RGR, and ECI suggest that chemical and physical changes may be occurring during the growing season. As predicted by Waldbauer (1968) and Scriber and Slansky (1981), RCR was significantly greater and ECI was significantly lower for budworms feeding on late season foliage than for those feeding on early season foliage in 1981. Despite this apparent effort to compensate for a suboptimal food source, the budworm larvae feeding on late season foliage were unable to complete their development.

The overall pattern of decreased RGR and ECI and the survival rate of the larvae feeding on middle season foliage in 1982 are comparable to those of the 1981 experiments. The decrease in RCR from the early to the middle season experiment does not follow the 1981 pattern. This may be due to chemical or physical feeding deterrents that could not be overcome by the budworm larvae.

Budworm larvae feeding on middle and late season foliage experience retarded development and mortality, though many feed as long as successful larvae that feed on early season foliage. These findings are consistent with those of Heron (1964), who studied *C. occidentalis* feeding on mature white spruce needles.

The feeding behavior of *C. occidentalis* appears to be adapted for making the most of the nutrients provided by the foliage of its host early in the growing season, while avoiding the physical and chemical defenses that may increase as the foliage matures. Studies of the physical and chemical changes in the foliage of these host trees as the growing season progresses are needed to better understand the feeding behavior of the western spruce budworm.

Acknowledgment

Work leading to this publication was funded in whole or in part by a program sponsored by the USDA Forest Service entitled Canada/United States Spruce Budworm Program–Science and Education Administration Agreement 59-2042-1-3-013-0.

Literature Cited

BEAN, J. L., AND H. O. BATZER. 1957. Mean head width for spruce budworm larval instars in Minnesota and associated data. J. Econ. Ent. 50:499.

HERON, R. 1964. The role of chemotactic stimuli in the feeding behavior of spruce budworm larvae on white spruce. Canadian J. Zool. 43:247–269.

SCRIBER, J.M., AND F. SLANSKY, JR. 1981. Nutritional ecology of immature insects. Ann. Review Ent. 25:183–221.

SHEPHERD, R. F. 1983. A technique to study phenological interactions between Douglas-fir buds and emerging second instar western spruce budworm. Pages 17–20 *in* Proceedings of the CANUSA workshop, Forest Defoliator-Host Interaction: a comparison between spruce budworm and gypsy moth. New Haven, Connecticut.

WAGG, J. W. B. 1958. Environmental factors affecting spruce budworm growth. Forest Lands Research Center. Corvallis, Oregon. Research Bulletin 11. 27 pp.

WAGNER, M. R., AND E. A. BLAKE. 1983. Western spruce budworm consumption-effects of host species and foliage chemistry. Pages 49–54 *in* Proceedings of the CANUSA Workshop, Forest Defoliator-Host Interaction: a comparison between spruce budworm and gypsy moth. New Haven, Connecticut.

WALDBAUER, G. P. 1968. The consumption and utilization of food by insects. Adv. Insect Physiol. 5:229–288.

WARING, R. H., W. G. THIES, AND D. MUSCATO. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci. 26(1):112–117.